*Journal of Research on the Lepidoptera* 14(4):216-232, 1975

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# POST-PLEISTOCENE ENVIRONMENTS AND MONTANE BUTTERFLY RELICTS

## ON THE WESTERN GREAT PLAINS

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For several reasons, a knowledge of the paleobotany of the western Great Plains has become increasingly important in understanding its butterfly fauna. Recent studies of many of its regional faunas (Brown *et al.*, 1957; Conway, 1966; Defoliart, 1956; Ferris, 1970a, 1970b, 1971; Johnson and Nixon, 1967; Johnson, 1972 (1973), 1975a; Nordin, 1967, 1968; Puckering and Post, 1960; and Scott, Ellis, and Eff, 1968) have placed a proper emphasis on the montane character of butterflies populating its non-riparian scarp woodlands and remaining climax coniferous forests. A rationale is needed to characterize these faunas in relation to their own elements as well as other faunas in the Nearctic (A. B. Klots and F. M. Brown, pers. com.). It is important to know whether they represent dispersal eastward from the Rocky Mountains, or if they are relicts of a former, more extensive, montane association in which unique allopatric populations of some montane Nearctic butterfly species occur, representing extreme divergence as peripheral populations. Similarly, understanding current ecological changes effecting their decline requires a knowledge of their probable origins (Johnson, 1976a).

Expanding distributional knowledge of taxa described from these areas, research presented in taxonomic studies (Ferris, 1973; Johnson 1976b, 1976c; Johnson and Balogh, 1976; Perkins and Perkins, 1967), and the recognition of important biological

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distinctions in some populations (Klots, 1975; and pers. com.) has indicated that many, if not most, of these scattered montane faunas are more related to each other than to faunas in the mountain ranges to their west. Thus, it is important to present paleobotanical evidence establishing this former montane association and to comment on its significance.

## DISCUSSION

The major remaining conifer forest and montane areas of the Great Plains occur from western Nebraska northward. They include the Black Hills of South Dakota, the Pine Ridge of Nebraska, the Cheyenne Ridge of Nebraska and Wyoming (called the "three great pine relicts" by Clements, 1945) and the more limited scarps along the Niobrara River in Nebraska and the Little Missouri River in Montana and North Dakota. Of these, only the Black Hills remains in a climax condition.

The history of these areas, and thus a major part of the history of the Great Plains, is best understood by presenting a vegetative chronology since the Wisconsin glaciation. This evidence can then be used to explain the occurrence of the montane elements in its butterfly fauna:

*The late Miocene, Pliocene, and early Pleistocene glaciations:*

In the late Miocene and Pliocene the entire area was open woodland (savannah), with *Cedrella* (Meliaceae), and early *Celtis, Quercus, Mahonia, Pinus, Artemisia, Ambrosia,* and many *Asteraceae.* Montane areas, like the uplifted Black Hills, were coniferous forest and remained so throughout the four glaciations of the Pleistocene. The ice advances and interglacial episodes caused floral fluctuations probably not unlike those of the Wisconsin glaciation described below, which are most important in understanding present faunas.

*Source:* Wells, 1970.

*The developing Wisconsin* (before 20,000 years ago):

Boreal forests proceeded in bands before the glaciers. Periglacial winds formed a sand dune desert in central Nebraska from sand blown in from the Ogallala formation of the northern Great Plains. The Pine Ridge, Cheyenne Ridge, and other present-day uplands were not exposed at this time, but were in fact buried.

*Sources:* Schuchert, 1955; Smith, 1965; Wright, 1970.

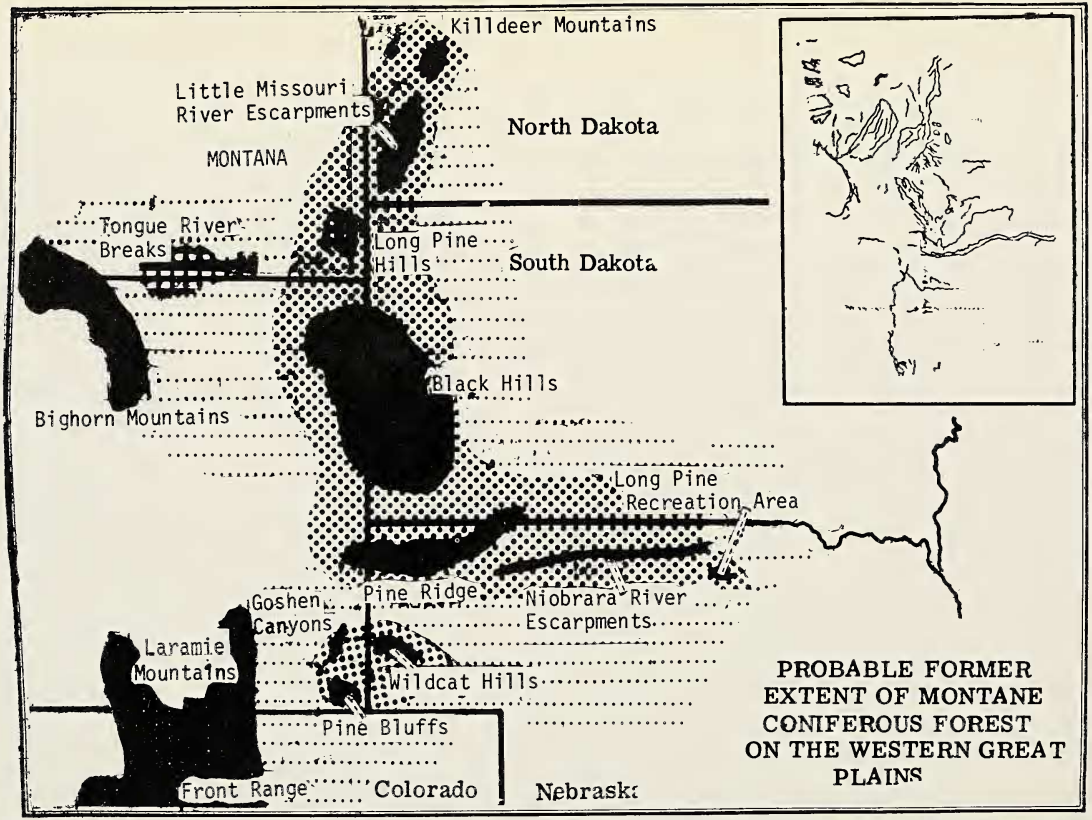



Fig. 1.—Map of western Great Plains area showing probable former extent of coniferous forest following the retreat of the Wisconsin glacier (dark stiples) and probable areas of pine-juniper open woodland during the same period (light stipled lines). Blackened areas represent present areas affording montane environments. Black areas with white cross-hatching represent areas of the Rocky Mountains. Areas of black cross-hatching show coniferous areas whose butterfly faunas are unknown. To the right above the title: the same region with lines representing present occurrence of scarp woodlands supporting pine (*Pinus ponderosa* Laws.) subclimax. The latter is the base map for noting butterfly distributions.

*The full-glacial Wisconsin* (14-20,000 years ago)

Boreal forest extended west to northeastern Kansas and northward across central Nebraska, but was prevented from reaching the Black Hills by the sand dunes. Instead, it continued westward across northwest South Dakota and north-central Wyoming. Montane *Pinus* climax forest covered the uplands westward. The present-day Pine Ridge, Cheyenne Ridge, and western North Dakota areas had now been exposed as uplands by the continual movement of loess eastward. Lowland pine-juniper open woodland occurred concentrically around the upland forests.

*Sources:* Wright, 1970; Wright and Ruhe, 1965.

*The early glacial retreat* (11-12,600 years ago):

Glacial retreat ended the periglacial winds. The sand dunes gave way to boreal forest which proceeded west to the present Black Hills. There, and in the Pine Ridge, Cheyenne Ridge, western North Dakota association, Niobrara River area, and associated lowland savannahs, it intermixed with montane coniferous forests. Contributed were still-surviving *Betula lenta* L., *B. papyrifera* Marsh., *Populus tremuloides* Michx., *Quercus macrocarpa* Michx., *Ostrya virginiana* Willd., *Ulmus americana* L. (pl. Clayt.), Willd., and *Corylus americana* Walt. The Bighorn Mountains were connected to the Black Hills by a moist (compared to today) *Pinus-Juniperus* savannah.

*Sources:* Morgan, 1963; Nixon 1967; Wells, 1970; Wright, 1970; Wright and Ruhe, 1965.

*Mid-glacial retreat* (10,000 years ago):

Further glacial retreat caused destruction of the boreal forest. Relicts survived in the Black Hills, Pine Ridge, and Niobrara escarpments. The extensive interplay of coniferous forest, open woodland, and prairie began. Montane coniferous areas were now nearly as shown in Figure 1.

*Sources:* McIntosh, 1961; Morgan, 1963; Nixon, 1967; Wells, 1970.

*Post Wisconsin—the warm postglacial interval* (9,500 to 1700 years ago):

Vast *Pinus* climax forests were evident as indicated in Figure 1.

*Pinus* dominated pine-juniper open woodland covered the present Sandhills of Nebraska and perhaps west-central North and South Dakota. Moist open woodland, predominantly *Juni-*

*perus* with some *Pinus,* connected the Laramie Mountains and Cheyenne Ridge, and the Bighorn Mountains and the Black Hills. A trend toward aridity began at the end of this period.
*Sources:* Deevy and Flint, 1957; Wells, 1970.
*The woodland to semi-desert transition* (1700-200 years ago):

Continuous coniferous forest began to receed. Pine climax retreated upland leaving subclimax relicts throughout various escarpments, but a climax forest in the Black Hills. In the face of increased aridity and prairie fires, open woodland began to give way to prairie.
*Source:* Wells, 1970.
*Demise of the conifers* (200 years ago to the present):

Continuous juniper and pine-dominated open woodlands came to an end. Conifers became nearly extinct in most areas, except remaining montane uplands. Mixed prairie and short-grass prairie disclimax prevailed over most areas; pine relicts remained limited to scarp woodland or the Black Hills.
*Sources:* Clements, 1945; Weaver and Albertson, 1956; Wells, 1965, 1970.

Figure 1 illustrates the probable maximum extent of former coniferous forest and pine-juniper open woodland on the western Great Plains in relation to existing nonriparian scarp woodlands. Distributions of species and subspecies endemic to these coniferous forests biomes are shown in figures 2 and 3. Figures 4 through 6 illustrate ranges of other montane entities still inhabiting the region, and probable relicts of two earlier fauna-influencing periods.

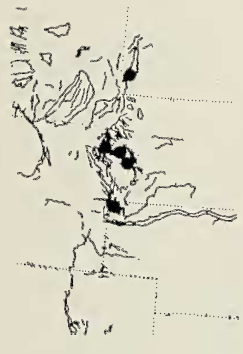
Examination of these data in relation to the chronology of paleobotanical events indicates evidence of five major elements influencing the existing butterfly fauna and its affinities:

1. Relicts of the boreal invasion and its associated deciduous flora (*L. eurydice* ssp., *P. batesii, N. vau-album j-album*).
2. Relicts of the extensive montane coniferous climax after the recession of the glaciers (*C. siva, C. meadii, C. alexandra krauthii, E. lucilius afranius, E. persius fredericki, E. ausonides palaeoreios, E. a. bernadetta, E. amyntula valeriae, G. piasus, H. pahaska pahaska, L. weidemeyerii oberfoelli, L. rubidus longi, N. ridingsii, N. menapia, P. phoebus dakotaensis, P. indra, P. muticaudatus, P. sisymbrii nordini, P. icarioides lycea, P. shasta minnehaha, P. satyrus, S. callippe, S. edwardsii, S. zerene*).

Hesperia pahaska pahaska Leussler

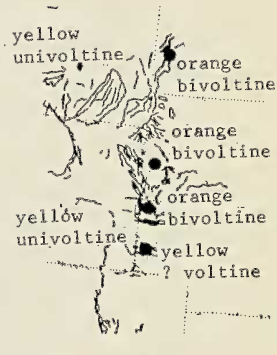
Erynnis lucilius afranius (Scudder and Burgess)

Erynnis persius fredericki H. A. Freeman



Euchloe ausonides palaeoreios Johnson

Pieris sisymbrii nordini Johnson




Colias alexandra complex

Fig. 2.—Distributions of species (includes only *Hesperia pahaska*) and subspecies (others) whose type localities are in one of the disjunct relict woodlands. Those clearly endemic are shown as such and usually represent montane coniferous forest entities. Others with more expansive distributions are usually montane grassland entities. Black lines on map indicate location of existing scarp woodlands in the region.

*Limenitis weidemeyerii oberfoelli* Brown

*Lycaena rubidus longi* Johnson and Balogh

*Plebejus shasta minnehaha* (Scudder)

*Euphydryas anicia bernadetta* Leussler

*Parnassius phoebus dakotaensis* Eisner

Fig. 3.—Same as Fig. 2.

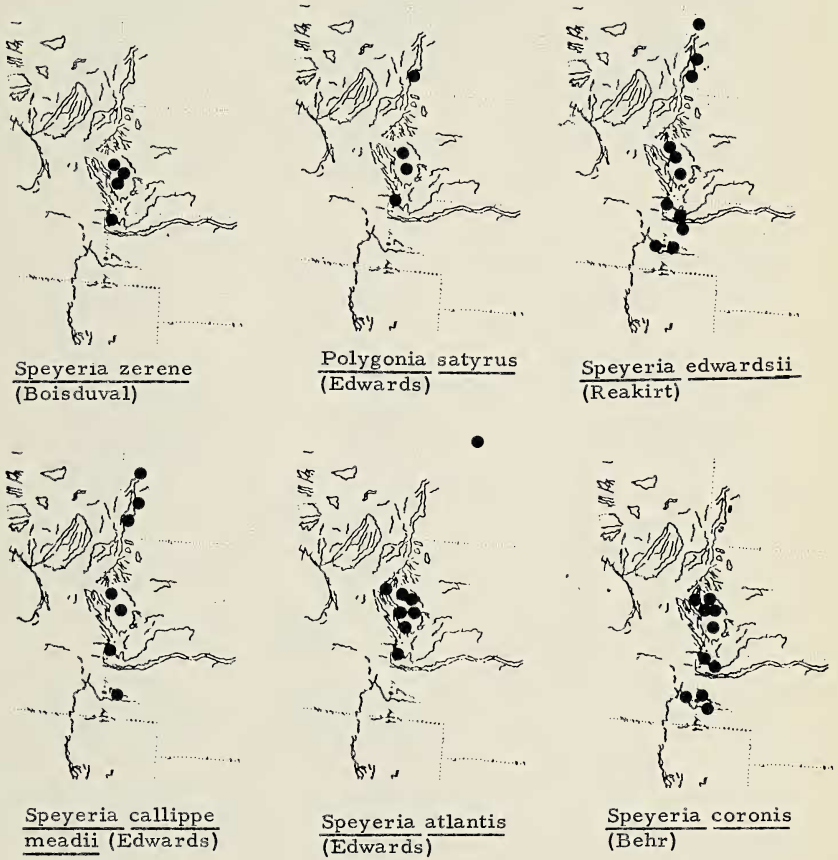



Fig. 4.—Distributions of other montane butterflies on the western Great Plains in relation to existing scarp woodlands.

Papilio multicaudatus
Kirby

Papilio zelicaon
Lucas

Papilio rutulus
Boisduval

Papilio indra
Reakirt

Papilio bairdii
brucei Edwards

Neophasia menapia
(Felder and Felder)

Fig. 5.—Distributions of other montane butterflies on the western Great Plains in relation to existing scarp woodlands.

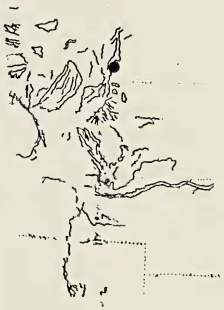
Callophrys (Incisalia) eryphon (Boisduval)

Callophrys (Mitoura) siva (Edwards)

Plebejus icarioides lycea (Edwards)

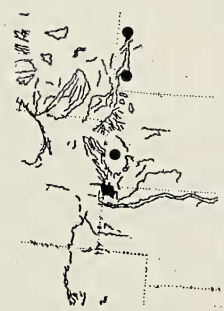
Glaucopsyche piasus (Boisduval)

Oeneis uhleri (Reakirt)



Cercyonis oetus oetus (Boisduval)

Neominois ridingsii (Edwards)



Cercyonis meadii (Edwards)

RELICTS OF FORMER EASTERN DECIDUOUS FOREST and NORTHWARD MONTANE INVASIONS

Phyciodes batesii (Reakirt)
Nymphalis vau-album j-album (Boisduval & LeConte)
Lethe eurydice (Johannsen)
.....
Asterocampa celtis antonia (Edwards)

Fig. 6.—Distributions of other montane butterflies on the western Great Plains in relation to existing scarp woodlands. Bottom right: listing of relict deciduous forest entities found in the Pine Ridge and representing extreme allopatry from their normal range.

3. Relicts of the northward dispersal of western montane entities (those above [2] but obviously *A. c. antonia*).
4. Relicts of montane entities once dispersed throughout the vast open woodlands (*C. siva, C. alexandra* ssp., *L. eurydice* ssp., *L. rudibus longi, P. multicaudatus, P. shasta minnehaha, S. edwardsii*).
5. The pattern of retreat of the coniferous forest at the beginning of the current aridity and fire-influenced period (all of the above, determining existing ranges).

These relationships show patterns important in interpreting the origin and faunal character of the insects of the region. All entities with habitats characteristic of montane coniferous forest, and with type localities within one of the now disjunct pine relicts, show a north-south distributional relationship within the former coniferous forest belt. Some are still found eastward along the Niobrara River where some limited scarp woodlands still support montane butterflies. Almost conversely, such entities, whose present distributions span the east-west arid basins, are grassland-related species, probably indicating the role of the open woodland in maintaining their ranges during the demise of the conifers, when montane forest entities retreated upland. Vast open woodland formerly in the Nebraska Sandhills, south of coniferous forest now isolated along the Niobrara River, figures as the origin of montane-related species which still occur there, in isolated and often unique environs like the post-climax prairie (Pool, 1914; Tolstead, 1941). In no case does a taxonomically distinct entity described from a montane conifer niche in the region show its primary relationship westward to the Rocky Mountains.

The most limited relict, small scarps which remain of the Cheyenne Ridge, contains montane representatives mostly with a northward relationship. However, some of its plains-adapted montane species evidence distinct interaction with populations clearly dispersed eastward from the Rocky Mountains. In strongly polymorphic *Colias alexandra* Edwards, evidence from Ferris (1973) and A. B. Klots (pers. com.) indicates the unique bivoltine and "orange" population called *C. a. krauthii* in the Black Hills does not extend southward and include the Cheyenne Ridge. Instead, a "yellow" population (of unclear voltinism) occurs here which seems more related to the "yellow" univoltine populations (called *C. a. alexandra*) on the plains sur-

rounding the Front Range in Colorado. Similarly, *Lycaena rubidus* Behr occurring on the plains south of the Pine Ridge shows purely northward related populations (*L. r. longi*) only in the pine-forested canyons of the region. Remaining populations on the plains, or in the limited remnants of the Cheyenne Ridge in Wyoming, show evidence of secondary intergradation with *L. r. rubidus* of the Rocky Mountains which has established many plains populations in eastern Colorado and Wyoming. The evidence of secondary intergradation in plains populations south of the Pine Ridge is shown in the geographic affinities of genitalic and wing pattern traits illustrated in Figure 7.

The great influence of the former extent of coniferous forest in the region can also be illustrated by the ranges and affinities of other montane species occurring on the Great Plains, but which have apparently not undergone extreme speciation (or perhaps simply have not been studied). Their distributions are shown in Figures 4 - 6.

Faunal resemblance formulae (Long, 1963) were used to compare the entire faunas of each relict area in this study and the mountain ranges in Colorado and Wyoming (Johnson, 1968). Results of such comparisons agree with the general affinities indicated by the ranges of individual taxa (The Pine Ridge relates to the Black Hills first, the Bighorn Mountains second; the Black Hills relates to the Big Horn Mountains first; the Cheyenne Ridge relates to the Pine Ridge first) but were not deemed as useful in illustrating real relationships. Their values are greatly prejudiced by the unique admixtures of biota in these areas caused by the incursion of prairie biomes into the scarp woodlands, the occurrence of alpine environs only in the Black Hills and Bighorn Mountains, and the infusion of southern-related species into the river drainages of Colorado and western Nebraska.

Apparent relict populations of butterflies representing earlier vegetative events in the region were also noted in the study areas and further attest to these uniquely vegetated scarp woodlands providing refugia for species not characteristic of the surrounding plains. In the Pine Ridge, a curious *Polygonia "hylas"* (Edwards) [the name *hylas* is presently of uncertain relationship with more northern *faunus* (Edwards) but has been traditionally used for Rocky Mountain populations of the complex] or extremely green *P. progne* (Cramer) occurs in the same areas as birch relicts. Birch (*Betula* sp.) is the northern larval food-

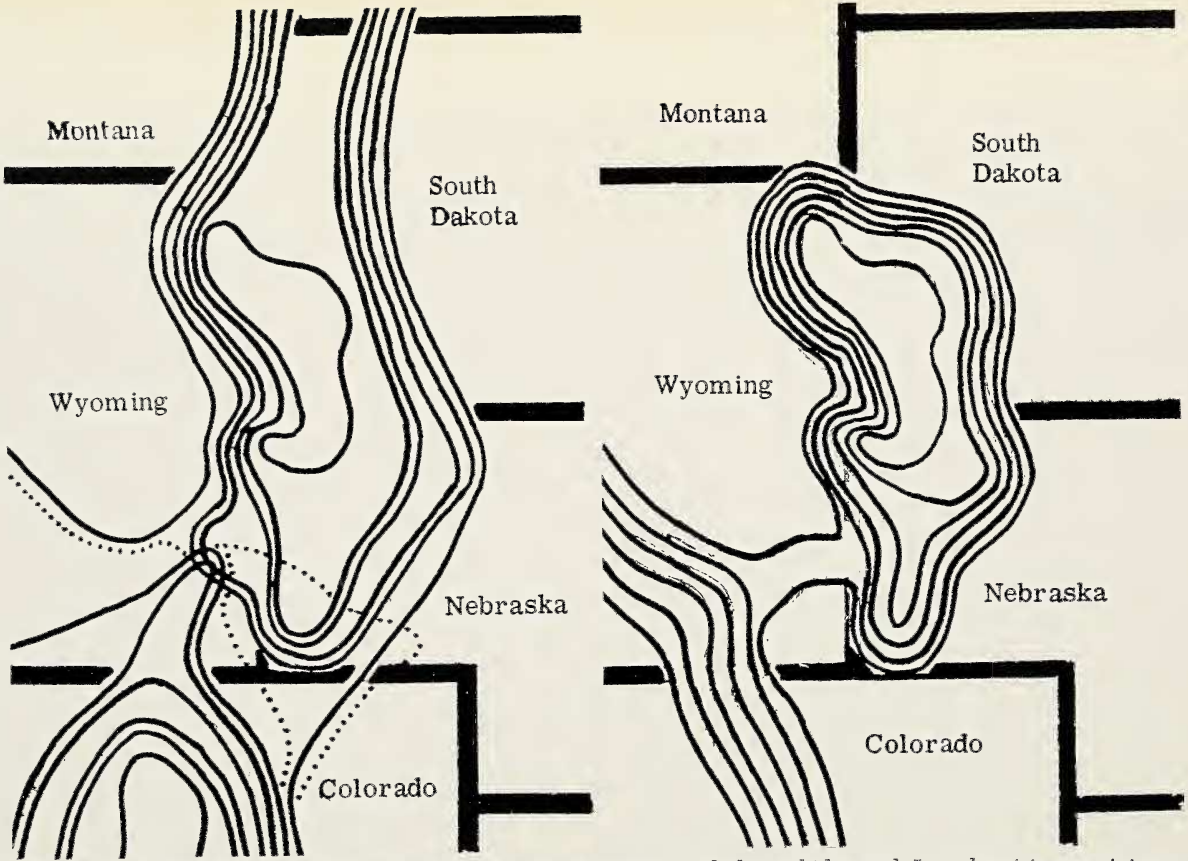



Fig. 7.—Evidence of slight secondary intergradation between *Lycaena rubidus rubidus* and *L. r. longi* in remaining populations on the plains grasslands. Each contour line represents two morphological traits in common, dotted lines one trait in common. Right: Geographic affinities of 23 male genitalic traits on 183 specimens from 62 localities. Left: Geographic affinities of 56 traits of the dorsal and ventral wing surfaces (males) on 727 specimens from 94 localities. Figure derived as a detail from Nearctic affinities in Johnson and Balogh, 1975.

plant of the *P. faunus- P. hylas* complex.

Also, three deciduous forest entities (*Phyciodes batesii* and *Nymphalis vau-album j-album* of eastern origin, and *Asterocampa celtis antonia* of southern origin) occur in the river bottoms of the Pine Ridge canyons. These are relicts of the westward deciduous movement and the northward invasion of southern montane entities respectively. Most interestingly, plains river bottom populations of *A. celtis* represent the nominate subspecies *celtis* (Boisduval and LeConte) which is of eastern affinity. The uniqueness of the canyon populations was confirmed by studying and rearing the larval stages [Johnson 1972 (1973)]. Also of importance is the occurrence of an extremely allopatric and disjunctly distributed subspecies of eastern *Lethe eurydice* Johannsen along the streams in the deep escarpment canyons. This population, isolated from the formerly most western population of the species, *L. e. fumosa* Leussler, is clearly a relict of the former westward extension of the eastern deciduous forest. Unfortunately, many areas in the region highly suited for such relicts have been ill-studied by lepidopterists and our knowledge of their occurrence is limited to only those areas which have received intensive local sampling. Thus, individuals of the above species (and others) may also occur northward in the present-day disjunct conifer woodlands, as do many of the montane species mentioned earlier.

## CONCLUSIONS

These data support three conclusions important to the history of butterfly speciation in the central and western Nearctic Realm.

1. The montane faunas of the remaining coniferous forests on the western Great Plains represent relicts of former, more extensive populations (not merely eastward dispersal from the mountains) and have a disjunct relationship to each other as opposed to the mountains to their west. 2. These same areas support allopatric populations of butterfly species from eastern and southern origins which are relicts of other vegetative invasions of the region. 3. This ancient montane and coniferous forest area should be considered as having formed a distinct area of speciation in the evolution of the present butterfly faunas of the Rocky Mountains and to a lesser extent those of eastern deciduous forest areas of North America.

## ACKNOWLEDGMENTS

I am grateful to Drs. Alexander B. Klots and F. Martin Brown (American Museum of Natural History) for originally discussing the need for this research with me, and to Dr. Klots for reviewing the manuscript. Particular debt is owed Dr. Frederick H. Rindge (American Museum of Natural History) for use of facilities and advice in investigating taxonomic problems. Thanks are due Mr. Eric Quinter (American Museum of Natural History) for critique, Dr. Lee D. Miller (Allyn Museum of Entomology, Sarasota, Florida) for permission to reproduce from a paper in press there, and Dr. Charles A. Long (Museum of Natural History, University of Wisconsin, Stevens Point) for the museum's support of this research.

## SPECIAL NOTES CONCERNING FORMAT IN THIS PAPER

I have included the authors' names for each taxon on the maps in the figures.

This seemed more ideal than citing them the first time they were used in the text 1. because of the number of names in the paper 2. the fact that some are mentioned in both species or subspecies contexts at times 3. the variance in degree of study in some of these groups taxonomically.

Thus, the only authors' names mentioned in the text are in use for the first time at variance with those in the figures (e.g. when a species is discussed, but a specific trinomen is cited in the figures). Therefore, the taxonomic names in the figures form a consistent usage for the region, dependent on the degree of study each group has received by entomologists.

## LITERATURE CITED

BROWN, F. M., D. EFF and B. ROTGER. 1957. Colorado Butterflies. *Denver Mus. Natur. Hist.*, Denver, 368 pp.

CLEMENTS, F. E. 1949. *The Dynamics of Vegetation*. H. W. Wilson, New York, xxiii + 296 pp.

CONWAY, P. J. 1966. A quick collecting trip to the Black Hills. *Newsl. Assoc. Minn. Entom.* 1 (1): 16-19.

DEEVY, E. S. and R. F. FLINT. 1957. Postglacial hypsithermal interval. *Science*, 125: 182-184.

DEFOLIART, G. R. 1956. An annotated list of southeastern Wyoming Rhopalocera. *Lepid. News* 10 (3-4): 165-175.

EMMEL, T. C. 1969. Taxonomy, distribution and biology of the genus *Cercyonis* (Satyridae). I. Characteristics of the genus. *J. Lepid. Soc.* 23 (3): 165-175.

FERRIS, C. D. 1970a. A checklist of the Rhopalocera of eastern Wyoming. *Mid-Contin. Lepid. Ser.* 1 (10): 1-11.
———. 1970b. Collecting spring diurnal Lepidoptera in southeastern Wyoming. *Mid-Contin. Lepid. Ser.* 1 (12): 6-10.
———. 1971. An annotated checklist of the Rhopalocera of Wyoming. *Agric. Exper. Stat., Univ. Wyo. Sci. Monog.* 21, 64 pp.
———. 1973. A revision of the *Colias alexandra* complex (Pieridae) aided by ultraviolet reflectance photography with designation of a new subspecies. *J. Lepid. Soc.* 27 (1): 57-73.
JOHNSON, K., and E. S. NIXON. 1967. The Rhopalocera of northwestern Nebraska. *Amer. Mid. Nat.*, 78 (2): 508-528.
JOHNSON, K. 1972 (1973). The butterflies of Nebraska. *J. Res. Lepid.* 11 (1): 1-64.
———. 1976a. Prairie and plains disclimax and disappearing butterflies. *Atala, Memoir No. 1, Xerces Society* (in press).
———. (ms. 1968) The faunal resemblances of butterflies of the western Great Plains, southern and central Rocky Mountains. *Project in Quantitative Biology, Univ. Wisc., Stevens Point.*
———. 1976b. Concerning the name *Anthocaris coloradensis* Hy. Edwards with designation of a new subspecies (Pieridae). *J. Lepid. Soc.* 30 (4): in press.
———. 1976c. A new subspecies of *Pieris sisymbrii* from western Great Plains relict forests (Pieridae). *J. Lepid. Soc.* 30 (3): in press.
JOHNSON, K., and G. BALOGH. 1976. A revision and taxonomic analysis of the nearctic *Lycaena rubidus* complex. *Bull. Allyn Mus. Entomol.* (in press).
KLOTS, A. B. 1975. *in* HOWE, W. (coordinating ed.) *The Butterflies of North America.* Doubleday and Company, Inc., Garden City, xii, 633 p., 97 pls.
LONG, C. A. 1963. Mathematical formulas expressing faunal resemblance. *Trans. Kans. Acad. Sci.* 66 (1): 138-140.
McINTOSH, A. C. 1931. A botanical survey of the Black Hills of South Dakota. *Black Hills Eng.* 19:159-276.
MORGAN, G. 1963. Relict populations of *Betula lenta* L. in northwestern Nebraska. Unpublished M.A. thesis, Univ. Nebr., Omaha.
NIXON, E. S. 1967. A vegetational study of the Pine Ridge of northwestern Nebraska. *Southwest. Nat.* 12 (2): 134-145.
NORDIN, J. S. 1967. Hesperiidae records for South Dakota. *Newsl. Assoc. Minn. Entom.* 1 (4): 90-92.
———. 1968. 1966 Lycaenidae records for South Dakota. *Bull. Assoc. Minn. Entom.* 2 (3): 60-61.
PERKINS, S. F., and E. M. PERKINS. 1967. Revision of the *Limenitis weidemeyerii* complex with description of a new subspecies (Nymphalidae). *J. Lepid. Soc.* 21 (4): 213-234.
POOL, R. J. 1914. A study of the vegetation of the sandhills of Nebraska. *Minn. Bot. Studies* 4:189-312.
PUCKERING, D. L., and R. L. POST. 1960. *Butterflies of North Dakota (North Dakota Insects)*, 1:32 pp. North Dakota State University, Fargo.
SCHUCHERT, C. 1955. *Atlas of paleographic maps of North America.* John Wiley and Sons, Inc. New York. 177 pp.
SCOTT, J. A., S. L. ELLIS, and J. D. EFF. 1968. New records, range extensions, and field data for Colorado butterflies and skippers. *J. Lepid. Soc.* 22 (3): 159-171.
SMITH, H. T. U. 1965. Dune morphology and chronology in central and western Nebraska. *Ecol. Monog.* 12:255-292.
TOLSTEAD, W. L. 1941. Vegetation of the northern part of Cherry County, Nebraska. *Jour. Geol.* 73:557-578.

WEAVER, J. E., and F. W. ALBERTSON. 1956. *Grasslands of the Great Plains*. Johnsen Publ. Comp., Lincoln, Nebraska.

WELLS, P. V. 1970a. Vegetational history of the Great Plains: a post-glacial record of coniferous woodland in southeastern Wyoming. *in*: Pleistocene and recent environments of the central Great Plains (Dort, W. D., and J. K. Jones, Edts.). *Dept. of Geol., Univ. Kansas, Spec. Publ.* 3:185-202.

———. 1970b. Historical factors controlling vegetation patterns in the cenral plains region of North America. *in*: Pleistocene and recent environments of the central Great Plains (Dort, W. D., and J. K. Jones, Edts.). *Dept. of Geol., Univ. Kansas, Spec. Publ.* 3:211-221.

WRIGHT, H. E., JR. 1970. Vegetational history of the central plains. *in*: Pleistocene and recent environments of the central Great Plains (Dort, W. D., and J. K. Jones, Edts.). *Dept. of Geol., Univ. Kansas, Spec. Publ.* 3:157-172.

WRIGHT, H. E., JR., and R. V. RUHE. 1965. *The Quaternary of the United States*: Princeton Univ. Press. 922 pp.